GYNANDROPSIS, CLEOME, AND PODANDROGYNE

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The genus *Gynandropsis* was established by de Candolle[1] in 1824 and supplied with nine species indigenous to the tropics and subtropics of both hemispheres, largely segregates from the Linnaean *Cleome*. The separation of the two genera was based upon the "torus": that of the latter "*subhemisphaericus*," and that of the former "*elongatus*." The separation was accepted generally and promptly, although with various phrasing by different authors ("Androphor kurz oder fehlend" *vs.* "Androphor entwickelt, deutlich"—Pax & Hoffman; "Stamens free" *vs.* "Stamens attached to the gynophore"—Fawcett & Rendle).

The flowers of *Cleome* and of *Gynandropsis*, as originally segregated, normally are hermaphrodite; hence the publication by Bentham[2] in 1845 of two monoecious species from the northern Andes, *G. coccinea* and *G. densiflora*, was of particular interest. Bentham described the inflorescences of his species as bearing staminate flowers toward the tip and pistillate flowers toward the base. Not until later was it appreciated that two of de Candolle's original species also possessed this character, namely *G. brachycarpa* and *G. hispidula*, also of the northern Andes.

In 1854, Turczaninov[3], apparently unaware of Bentham's publication, proposed several additional South American species of *Gynandropsis*, some of them synonymous with those of the earlier author. This article is particularly interesting, however, in the implied (but unfortunately not formally proposed) segregation of the hermaphrodite species into the section *Eugynandropsis*, and those with monoecious flowers into the sections *Hymenadenia* and *Gyradenia*. Although recognizing *Gynandropsis* merely as a section of *Cleome*, Triana & Planchon[4] also divided the Colombian species into two unnamed subsections having the flowers hermaphrodite or monoecious, respectively. Also noteworthy in this latter treatment is the description of *Cleome (Gynandropsis) decipiens*, a peculiar plant bearing large, simple leaves in contrast to the palmately compound leaves of other species of *Gynandropsis*. The discernment of these three early authors puts to shame their successors who ignored them for over three-quarters of a century.

In 1891, Pax[5] discarded *Gynandropsis* in favor of the earlier *Pedicellaria* Schrank[6], but in 1930 the former name was conserved by the Cambridge Congress[7], and the lectotype proposed as *G. pentaphylla* (L.) DC., a hermaphrodite species.

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[1] DC. Prodr. 1:237. 1824.
[2] Benth. Pl. Hartw. 160. 1845.
[3] Turcz. in Bull. Soc. Nat. Moscou 27^2:313. 1854.
[4] Tr. & Pl. Prodr. Fl. Novo Gran. 70. 1862.
[5] Pax, in Engl. & Prantl, Nat. Pflanzenfam. ed. 1. 3^2:223. 1891.
[6] Schrank, in Roemer & Usteri, Mag. 3:10. 1790.
[7] Int. Rules, ed. 3. 97. 1935.

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In 1930, Ducke[8] published the genus *Podandrogyne* from eastern Peru. Ducke appreciated the relationship of his genus to the monoecious species of *Gynandropsis* but, paradoxically, was handicapped, on the one hand, by the excellence of his study collection and, on the other, by ignorance of the fruiting habit of the species of monoecious *Gynandropsis*. Hence, the primary characters of his *Podandrogyne* were fruiting characters: "*Cleomoideis . . . differt replo nullo valvis post dehiscentiam irregulariter contortis.*" Ducke's illustration of *P. glabra*, the monotype, is excellent in detail of the simple-leaved (cf. *Cleome decipiens* Tr. & Pl.) species with monoecious flowers in an ebracteate raceme, with the peculiarly contorted replum (sic!) of the irregularly dehiscent silique. Also drawn with careful detail is a character apparently unappreciated by the author: the conspicuous membranaceous, funicular aril of the seed!

During the preparation of my account of Capparidaceae for the 'Flora of Panama,' compiled by Dr. Schery and myself[9], I have had the opportunity to examine numerous specimens of *Gynandropsis* from South America as well as from Panama, and have found it easy to demonstrate that all monoecious species of *Gynandropsis*, whether bearing simple or palmately compound leaves, produce fruit with the peculiar silique dehiscence and arillate seeds so well illustrated by Dr. Ducke. The fruit, however, is not actually without a replum, as may easily be observed from any specimen. But, except possibly in the case of *G. brachycarpa* DC., the pericarp appears to rupture irregularly without the customary abscission of the two valves, and the replum abjuncts at the apex, later undergoing the characteristic contortion. These features surely must have been displayed by the rich South American collections at Berlin, and it is difficult to understand how Pax & Hoffman[10] could see fit to erect a new subfamily, Podandrogynoideae, for the monotypic *Podandrogyne*, while leaving the numerous monoecious species within *Gynandropsis* of the Cleomoideae.

The Capparidaceae are a fascinating family which has not been studied effectively in its American representation since 1865[11]. Were I to undertake such a study, I am sure that I should return the hermaphrodite species of *Gynandropsis* to *Cleome*, since it would be an easy task to reveal the unreliable nature of the "torus" character, unsupported as it is by any other. The problem is one of considerable magnitude, however, and one which I must leave to another. Nevertheless, I do feel competent at the present time to append to this discussion a brief synopsis emending the genus *Podandrogyne* to include all monoecious species of *Gynandropsis*.

My study collection consists chiefly of specimens deposited in the herbaria of the Missouri Botanical Garden and the Chicago Natural History Museum, augmented by certain material from the U. S. National Herbarium and the Royal

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[8] Ducke, in Archiv. Jard. Bot. Rio Jan. 5:115. *pl. 7.* 1930.
[9] Woodson & Schery, in Ann. Missouri Bot. Gard. 35:75. 1948.
[10] Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2. 17b:208. 1936.
[11] Eichl. in Mart. Fl. Bras. 13^1:238. 1865.

Botanic Gardens, Kew. Types from continental European herbaria are represented by photographs prepared by J. Francis Macbride through the Rockefeller Fund.

PODANDROGYNE Ducke, emend.

PODANDROGYNE Ducke, in Archiv. Jard. Bot. Rio Jan. 5:115. 1930.

Gynandropsis DC. Prodr. 1:237. 1824, in part.

Erect or ascending, suffrutescent or suffruticose herbs; leaves alternate, simple or palmately compound, exstipulate; inflorescence racemose or corymbose, terminal, several- to many-flowered, bracteate or ebracteate; flowers monoecious, rarely andromonoecious or dioecious through abortion, the lower flowers pistillate, the upper staminate; calyx more or less deeply 4-parted, persistent or deciduous, sometimes more or less petalaceous; petals 4, more or less unequal, usually unguiculate; disc usually manifest, symmetrical or eccentric; fertile stamens 6, inserted on a short or moderately elongate, concentric or eccentric gynophore, the filaments somewhat unequal and declinate, the anthers dorsifixed near the base, accompanied by an abortive pistillode; fertile ovary borne upon a manifest, concentric or eccentric gynophore, the stigma capitate, sessile or stipitate, the ovules numerous, the accompanying staminodia greatly reduced, sagittate, borne upon a manifest androgynophore; fruit a dry, terete or somewhat compressed silique, usually dehiscing irregularly, the replum finally separating at the tip (except in *P. brachycarpa?*) and irregularly contorted; seeds cochleate-reniform, with a conspicuous lamellate, funicular aril.

Type species: PODANDROGYNE GLABRA Ducke, loc. cit. 1930.

a. Androgynophores included, concentric, the disc inconspicuous and essentially radial, not enlarged and conspicuous in fruit.
  b. Leaves palmately compound, usually 3- to 7-foliolate; calyx lobes cleft nearly to the receptacle; Costa Rica and Panama (to Peru?) .... 1. *P. chiriquensis*
  bb. Leaves simple; calyx campanulate, the lobes cleft about half or less to the receptacle; Colombia ..... 2. *P. decipiens*
aa. Androgynophores exserted, conspicuously eccentric through the unilateral development of a thick disc which is enlarged and conspicuous in fruit.
  b. Leaves palmately compound, usually 3- to 7-foliolate, or the uppermost or lowermost occasionally simple.
    c. Fruits linear-oblongoid, much longer than the androgynophore.
      d. Inflorescence corymbose, greatly contracted, not secund, erect; Colombia and Ecuador ..... 3. *P. coccinea*
      dd. Inflorescence racemose, relatively elongate, secund, somewhat cernuous; Venezuela ..... 4. *P. cernua*
    cc. Fruits broadly oblongoid to ovoid, about as long as the androgynophore or somewhat shorter.
      d. Plants densely pubescent; leaflets 5–9; lowermost flowers frequently perfect; inflorescence frequently with more or less persistent, foliaceous bracts; Colombia to Bolivia ..... 5. *P. brachycarpa*
      dd. Plants essentially glabrous; leaflets 3, or the lowermost or uppermost sometimes simple; flowers apparently always monoecious; inflorescence ebracteate; Colombia and Ecuador ..... 6. *P. gracilis*
  bb. Leaves simple.
    c. Inflorescence relatively elongate, secund, somewhat cernuous.
      d. Calyx lobes ovate to ovate-lanceolate, acuminate, pale green suffused with pink; fruits clavate-oblongoid, about as long as

the androgynophore or somewhat shorter; Colombia and Venezuela ..... 7. *P. macrophylla*

dd. Calyx lobes ovate-subreniform, obtuse, deep purple; fruits linear-oblongoid, about twice as long as the androgynophore; Colombia ..... 8. *P. polychroma*

cc. Inflorescence congested, not secund, erect; Colombia to Peru and adjacent Brazil ..... 9. *P. glabra*

1. PODANDROGYNE CHIRIQUENSIS (Standl.) Woodson, in Ann. Missouri Bot. Gard. 35:85. 1948.

Gynandropsis chiriquensis Standl. in Jour. Wash. Acad. 17:252. 1927.
Gynandropsis pulcherrima Standl. loc. cit. 253. 1927.

COSTA RICA: *Standley & Valerio 44560; Dodge & Thomas 5628; A. Smith H. 481; A. Smith P.C. 361; Skutch 3627.* PANAMA: *White & White 50; P. White 168; Seibert 138, 334; Woodson, Allen & Seibert 859; Woodson & Schery 539; Davidson 180; Allen 1650, 219, 2730, 4780, 4956; Hunter & Allen 552.*

Standley's primary distinction between *G. chiriquensis* and *G. pulcherrima* is based upon number of leaflets: five in the former and three in the latter. The Costa Rican specimens enumerated above all have three leaflets, and one may judge that the eleven additional Costa Rican specimens enumerated by Standley are constant to that number. Amongst the Panamanian specimens before me, three from the province of Chiriquí bear 3-foliolate leaves, and seven bear leaves which are 5- to 7-foliolate. Farther east, in the province of Coclé, three plants again bear 3-foliolate leaves. Since I have been able to discover no additional character to separate *G. chiriquensis* and *G. pulcherrima,* I am unwilling to maintain the two species separately, although they might be regarded as varieties with rather poor geographical differentiation.

Whether *P. chiriquensis* extends into northern South America is a subject for conjecture because of our meagre representation of the genus. Two specimens before me, however, will fall to that species in the key which I have prepared, although they differ from the Central American population in certain respects; both are 3-foliolate: *Pennell 14073,* from the department of Cusco, Peru, is the type specimen of *Gynandropsis Herrerae* Macbr. (in Field Mus. Publ. Bot. 4:168. 1929); at first glance strongly recalling Costa Rican *G. pulcherrima,* this plant differs in the slightly more coherent calyx lobes, thus recalling *Podandrogyne coccinea. Cuatrecasas 11497,* from Comisaría del Putumayo, Colombia, also will key to *P. chiriquensis,* the calyx being rather typical of the latter species, but the mature fruits are scarcely half as long. It may well be that these two sheets represent two distinct species, but I am inclined to consider hybridization of *P. chiriquensis* with such typically South American species as *P. coccinea* and *P. gracilis* as equally possible.

2. PODANDROGYNE **decipiens** (Tr. & Pl.) Woodson, comb. nov.

Cleome decipiens Tr. & Pl. Prodr. Fl. Novo Gran. 75. 1862.
Gynandropsis decipiens (Tr. & Pl.) Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2. 17b:218. 1936.

COLOMBIA: *Cuatrecasas 13685.*

This specimen, collected by Dr. Cuatrecasas on the Cordillera Occidental, Depto. del Valle, at 300 m. alt., is of particular interest since it apparently represents the first collection of this species since the type. I have not been able to examine the type, collected at Quindio, and it is not represented in the Macbride collection of type photographs; but our specimen agrees so thoroughly with Triana and Planchon's description that there can be little doubt of its identity. Our specimen in the herbarium of the Missouri Botanical Garden is represented by two sheets bearing identical data, and is of interest from the standpoint of leaf variation. In one sheet, the leaves are broadly ovate and cordate, while in the other they are less broadly ovate and rounded at the base.

3. PODANDROGYNE **coccinea** (Benth.) Woodson, comb. nov.

Gynandropsis coccinea Benth. Pl. Hartw. 160. 1845.
Gynandropsis aurantiaca Turcz. in Bull. Soc. Nat. Mosc. 27^2:315. 1854.

COLOMBIA: *Hartweg 888; Linden 814; Funck & Schlim 1648* (photo). ECUADOR: *Mexia 8443, 8444; Steyermark 54230.*

This species is the Colombian and Ecuadorian counterpart of the Central American *P. chiriquensis*, from which, beside the more important key characters, it may be distinguished by the greater connation of the calyx lobes.

4. PODANDROGYNE **cernua** Woodson, spec. nov.

Herba ca. 1.5 m. longa aut fortasse basi frutescens omnino glabra. Folia longe petiolata lamina 3-foliolata foliolis brevissime petiolulatis ellipticis subcaudato-acuminatis basi latiuscule acutis 9–13 cm. longis 3–5 cm. latis membranaceis petiolo ca. 7–10 cm. longo. Inflorescentia terminalis racemiformis sat elongata secunda multiflora ebracteata; pedicellis usque 2.5 cm. longis; floribus inferioribus femineis superioribus masculis. Florum masculorum calyx campanulatus laciniis ca. tertia parte connatis acutis ca. 5 mm. longus glaber ruber apice purpureus; petala oblongo-spatulata ca. 1 cm. longa salmonea; androphorium eccentricum basi disco carnoso unilaterali cinctum ca. 1 cm. longum; antherae 6 ca. 8 mm. longae filamentis subaequilongis. Flores feminei desunt. Siliquae immaturae lineares glabrae stigmate sessili stipitatae basi glandula peristente instructae.

VENEZUELA: Mérida: between Los Corales and Las Cuadras, alt. 1490–3210 m., March 25, 1944, *J. A. Steyermark 55772* (Herb. Chicago Nat. Hist. Mus., TYPE).

It is rather remarkable that the two Venezuelan species of *Podandrogyne*, this and *P. macrophylla*, both are characterized by secund inflorescences. From the latter species, *P. cernua* differs not only in its palmately compound leaves, but in the larger flowers and linear, shortly stipitate fruits.

5. PODANDROGYNE **brachycarpa** (DC.) Woodson, comb. nov.

Gynandropsis brachycarpa DC. Prodr. 1:238. 1824.
Cleome brachycarpa Vahl, ex DC. loc. cit. 1824, nom. nud. in synon.
Gynandropsis hispidula DC. loc. cit. 1824.

Cleome hirsuta R. & P. ex DC. loc. cit. 1824, nom. nud. in synon.
Gynandropsis densiflora Benth. Pl. Hartw. 160. 1845.
Gynandropsis phoenicea Turcz. in Bull. Soc. Nat. Mosc. 27^2:316. 1854.
Gynandropsis adenocarpa Turcz. loc. cit. 1854.
Cleome puberula Tr. & Pl. Prodr. Fl. Novo Gran. 71. 1862.
Cleome densiflora Benth. ex Tr. & Pl. loc. cit. 72. 1862.
Cleome densiflora β pallens Pl. & Lind. ex Tr. & Pl. loc. cit. 1862.
Cleome Macrothyrsus Tr. & Pl. loc. cit. 1862.
Cleome lateralis Tr. & Pl. loc. cit. 73. 1862.
Cleome brachycarpa Vahl, ex Tr. & Pl. loc. cit. 1862.
Pedicellaria Lehmannii Hieron. in Engl. Bot. Jahrb. 20, Beibl. 49:20. 1895.
Pedicellaria Ulei Gilg, in Engl. Bot. Jahrb. 40:421. 1908, nom. nud.
Gynandropsis Ulei Briq. in Ann. Cons. & Jard. Bot. Genève 17:385. 1914.
Gynandropsis Mathewsii Briq. loc. cit. 387. 1914.
Gynandropsis Jamesonii Briq. loc. cit. 388. 1914.
Gynandropsis puberula (Tr. & Pl.) Macbr. in Field Mus. Publ. Bot. 11:22. 1931.
Gynandropsis hirsuta Moldenke, in Phytologia 1:5. 1933.
Gynandropsis lateralis (Tr. & Pl.) Pax & Hoffm. loc. cit. 1936.
Gynandropsis macrothyrsus (Tr. & Pl.) Pax & Hoffm. loc. cit. 1936.

This rather formidable synonymy has accumulated primarily because of the variability of texture and quantity of indument of the collected specimens, but also because of the bracteate inflorescence of certain of them and the ebracteate appearance of others. The species evidently is a rather common one from Colombia to Bolivia, and has been collected repeatedly. Although such questions are solved better through study of living plants, I have come to the conclusion through study of the exsiccatae enumerated below that *P. brachycarpa* is characterized by inflorescence bracts which are rather irregularly caducous, the latter propensity accounting for the seeming biotic variability. The bracts also, as is normal, decrease in size from base to apex of the inflorescence, so that inflorescences in a late state of development, in which the lower bracts have been lost, appear to be completely ebracteate.

A more important feature of the species, which apparently has been overlooked by most students, is the propensity for the lowermost flowers of the inflorescence to be hermaphrodite, and not pistillate only as in the other species. This character, together with the bracts, might suggest this species as being possibly the most primitive of the genus, at least from a structural standpoint.

COLOMBIA: *Haught 1953; Dryander 2081; Arbelaez & Cuatrecasas 6181; Lehmann 7437* (photo); *Triana s. n.* (photo); *Triana s. n.* (photo); *Triana s. n.* (photo); *Funck & Schlim 1407* (photo). ECUADOR: *Steyermark 54295; Steyermark 54867; Skutch 4542; Eggers 14907; Penland & Summers 111; Jameson 461* (photo). PERU: *Vargas 524; Macbride 4213; Schunke 266; Poeppig 1530; Weberbauer 6653; Ule 6430* (photo); *Mathews 193* (photo); *Pavon s. n.* (photo). BOLIVIA: *Buchtien 2219; Cardenas 707.*

6. PODANDROGYNE **gracilis** (Tr. & Pl.) Woodson, comb. nov.

Cleome gracilis Tr. & Pl. Prodr. Fl. Novo Gran. 74. 1862.
Cleome gracilis β turgescens Tr. & Pl. loc. cit. 1862.
Cleome porphyrantha Tr. & Pl. loc. cit. 71. 1862.

Gynandropsis gracilis (Tr. & Pl.) Macbr. in Field Mus. Publ. Bot. 11:22. 1931.
Gynandropsis porphyrantha (Tr. & Pl.) Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. 17b:218. 1936.

COLOMBIA: *Cuatrecasas 8706; Goudot s. n.; Triana s. n.* (photo). ECUADOR: *Haught 2884; Steyermark 52853; Sodiro 68* (photo).

It is impossible for me to effect an absolute separation of this species and *P. brachycarpa*. Typically, as the preceding key suggests, the population which I call *P. brachycarpa* would appear amply distinct from the more northern *P. gracilis*. Amongst the specimens enumerated above, however, there is obvious intergradation, particularly with respect to indument, which might be construed as evidence of interspecific introgression through hybridization.

7. PODANDROGYNE **macrophylla** (Turcz.) Woodson, comb. nov.

Gynandropsis macrophylla Turcz. in Bull. Soc. Nat. Mosc. 27^2:314. 1854.

COLOMBIA: *Funck & Schlim 1210* (photo). VENEZUELA: *Steyermark 55821.*

Discussed previously with regard to *P. cernua.*

8. PODANDROGYNE **polychroma** Woodson, spec. nov.

Suffrutex erectus ca. 2 m. longus omnino glaber. Folia sat breviter petiolata lamina simplice late elliptica breviter acuminata basi late acuta ca. 20 cm. longa 10–11 cm. lata membranacea petiolo ca. 2.5 cm. longo. Inflorescentia terminalis racemiformis sat elongata secunda (?) multiflora ebracteata; floribus inferioribus femineis superioribus masculis; pedicellis usque 1 cm. longis. Florum masculorum sepala libera ovato-subreniformia obtusa ca. 5 mm. longa 7 mm. lata purpurea petala oblongo-obovata ca. 8 mm. longa rosea; androphorium eccentricum basi disco carnoso unilaterali cinctum ca. 1 cm. longum; antherae 6 ca. 8 mm. longae filamentis subaequilongis. Flores feminei desunt. Siliquae fusiformes glabrae ca. 10 cm. longae androgynophorio ca. 4 cm. longo basi glandula persistente instructo.

COLOMBIA: El Valle: Cordillera Occidental; vertiente occidental; Hoya del río Sanquininí, lado izquierdo, La Laguna, bosques, 1,250–1,400 m. alt., Dec. 10–20, 1943, *J. Cuatrecasas 15578* (Herb. Missouri Bot. Gard., TYPE).

This species is utterly unlike any other known to me in the shape and color of the sepals, and particularly in the very large and conspicuous gland at the base of the fruiting androgynophores. Unfortunately, the one inflorescence is well past prime; consequently its description as secund must await verification.

9. PODANDROGYNE GLABRA Ducke, Archiv. Jard. Bot. Rio Jan. 5:115. *pl. 7, fig. 9.* 1930.

Gynandropsis orba Macbr. in Candollea 5:359. 1934.
Podandrogyne pubescens Asplund, in Sv. Bot. Tidskr. 30:266. *fig. 1.* 1936.
Podandrogyne orba Macbr. in Field Mus. Publ. Bot. 13^2:988. 1938.

COLOMBIA: *von Sneidern 1684.* ECUADOR: *Steyermark 52654; Sodiro 67* (photo). PERU: *Weberbauer 6760; Killip & Smith 26125; Killip & Smith 29594; Killip & Smith 29480.* BRAZIL: *Ducke 19701* (photo).

Podandrogyne pubescens differs from typical *P. glabra* only in its copious indument, as far as I am able to judge. But in several of the specimens enumerated above, which superficially appear glabrous, traces of pubescence may be found, particularly upon the petioles and peduncles. *P. pubescens* might possibly be interpreted as a variety of *P. glabra,* but I am not willing to maintain it as a species at the present time.

Explanation of Plate

PLATE 8

Figs. 1–5. *Podandrogyne chiriquensis:* 1, habit; 2, seed; 3, dehisced fruit; 4, staminate flower; 5, pistillate flower.

Fig. 6. *Podandrogyne coccinea:* staminate flower.

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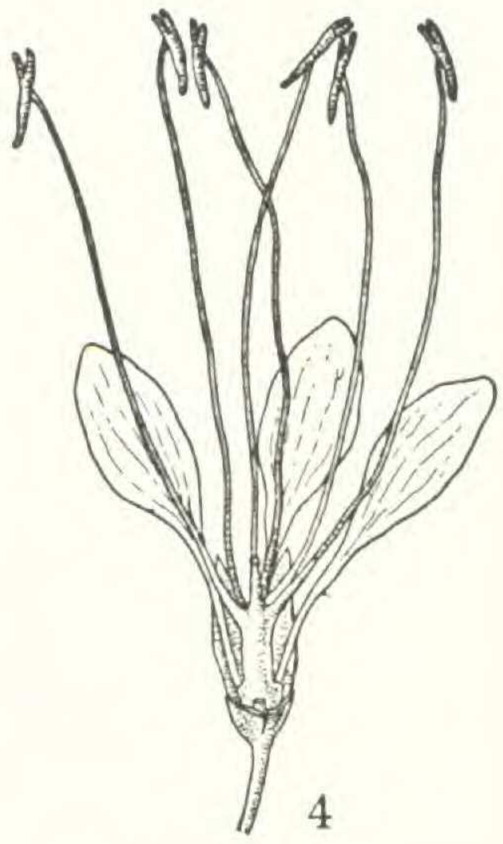

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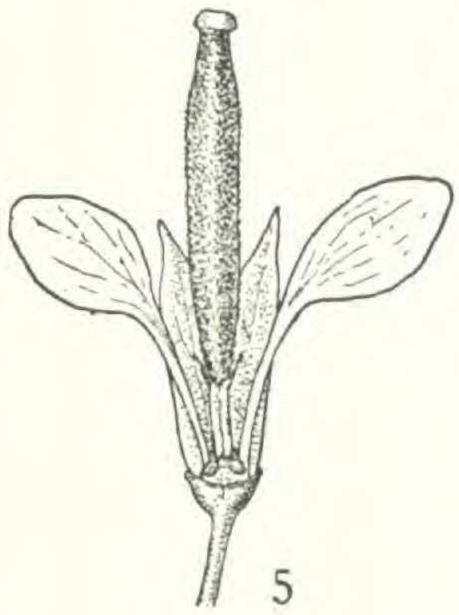

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6